Chapter 16

NUTRIENT CYCLING IN HEATHLANDS[1]

R.H. GROVES

INTRODUCTION

Nutrient cycling in shrublands does not differ essentially from that in other vegetation types, although in shrublands lower amounts of nutrients may be immobilized in wood than in a forest, for example. Shrublands may also be burnt more frequently than most vegetation types other than grasslands, so that nutrient cycles in shrublands may be perturbed more frequently.

Nutrient cycling generally has been the subject of a number of reviews (for example, Bormann and Likens, 1967), especially in woodlands (Ovington, 1962). Gimingham (1972) reviewed nutrient cycling in northwestern European heathlands dominated by *Calluna vulgaris*. This contribution extends that review to include information available not only for *Calluna* heathlands but also for Australian heathlands, and identifies some of the deficiencies in our knowledge of nutrient cycling in these communities. Unfortunately no results are available on nutrient cycling in South African fynbos — a heathland type closely comparable with the wetter end of the Australian heathland spectrum. Certain fluxes within the cycle for shrublands may be more significant for conservation of scarce nutrients than in some other vegetation types. Few generalizations are possible because of the paucity of the literature relative to that for certain other vegetation types, but some will be attempted.

A generalized scheme for cycling of those nutrients lacking a gaseous phase (so-called "sedimentary" nutrients) in shrublands is given in Fig. 16.1 and this forms the conceptual basis for much of what follows in the next three sections. Cycling of carbon, nitrogen and sulphur will differ from this scheme in some respects; nitrogen cycling will be described later. Inputs or accessions to the nutrient pool in the vegetation include rainfall and the accompanying dust particles and aerosols, together with the elements contained in unweathered parent rock and the several soil layers. Grazing and browsing animals may bring in nutrients as may alluvial material. Outputs or losses from the nutrient pool may include peat harvesting in northern European heathlands, movements of animals out of the area, volatilization in the case of some nutrients (e.g. nitrogen as ammonia), movement of smoke and ash particles when the vegetation is burnt, export of alluvial material, and solutes in run-off and deep drainage.

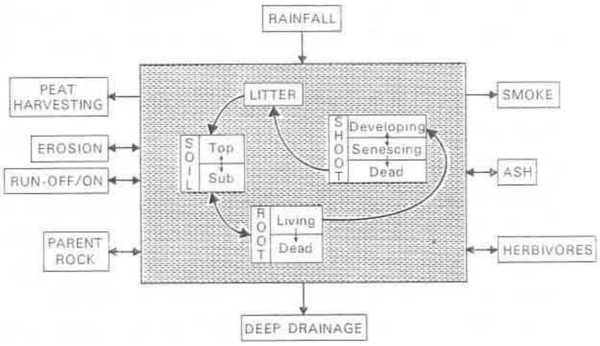

Fig. 16.1. Major inputs and outputs of sedimentary-type nutrients and their flow in a heathland soil–plant ecosystem.

Within the nutrient pool, fluxes occur at many levels — between soil horizons, between soil and plant roots, between roots and shoots, between developing and senescing tissue, and between litter and soil. In a strict sense, most of the inputs and outputs may also be considered fluxes. In what

[1] Manuscript completed February, 1977.

follows, however, I shall refer only to those dynamic balances in nutrients **within** the heathland system as fluxes, and inputs and outputs will be considered separately. An overall nutrient budget will then be presented.

Within plants some nutrients are relatively mobile, such as phosphorus, and some relatively immobile, such as calcium. The cycles for these two elements as examples of these two groups of nutrients are described in some detail and quantified wherever possible in the next two sections, which are then briefly compared and contrasted with nitrogen cycling in shrublands, the latter being a non-sedimentary cycle and involving a greater exchange between plant and atmosphere, both below and above ground. Generally, sedimentary cycles for elements such as phosphorus and calcium are more affected by man's activities than, say, carbon or nitrogen cycles (Bormann and Likens, 1967). A short discussion on sulphur and iron is also included because of the special significance of these elements to heathlands. Cycling of micro-elements will not be considered as they have yet to be shown to be in limiting supply for the growth of heath plants in the field, even though such plants often occur on soils in which the levels of some micro-elements are deficient for growth of crop and pasture plants, for instance, in southeastern South Australia.

PHOSPHORUS

Inputs

Rainfall

The phosphorus concentration of rainwater is generally low. For five sites in Britain, Allen et al. (1969) measured a range of 0.002 to 0.009 kg phosphorus ha^{-1} (cm of rain)$^{-1}$. Measurements of annual additions of phosphorus for a number of sites, mainly in Britain, are presented in Table 16.1, which is an extension of table 28 of Gimingham (1972). The level of phosphorus in rainwater may sometimes be too low for some analytical methods as, for example, Attiwill (1966) found. The low value for phosphorus in rainwater in southern England reported by Chapman (1967) may be explained in this way.

Parent rock

Wild (1961) analyzed 12 samples, collected from southeastern and northeastern Australia, of granitic or closely related parent rock and found a range between 0.039 and 0.096% phosphorus. None of the areas from which the samples were collected were typically heathlands, however, though granite is a common parent rock associated with such vegetation in southern Australia and South Africa. A range between 0.001 and 0.006% phosphorus for parent rock was found by Beadle (1962) for Hawkesbury Sandstone, which commonly supports heathland in the Sydney region of eastern Australia and which produces soils of extremely low fertility. Harwood (1972) summarized results of analyses of Precambrian rocks from southwestern Tasmania and found a mean of 0.03% phosphorus for 64 samples, mainly of quartz and schists. Several samples of quartz had no measurable phosphorus content. Rates of rock weathering and leaching are not known for these examples.

Soil

Total phosphorus levels in soil under heathland are low (Chapter 13) and are of the order of 0.002% phosphorus in the topsoil of podzolized sands in southern Australia. Though low, the soil reserve is a major source of phosphorus for the heathland ecosystem. By assuming a bulk density of 1.5 g cm^{-3} this gives a level of 45 kg ha^{-1} phosphorus in the top 15 cm of heathland soils in this region. This level is slightly higher than that reported by Chapman (1967) for southern England and is up to ten times lower than that for a range of heathland soils in northern Britain (Robertson and Davies, 1965), presumably because of the higher level of organic matter in the latter.

Other sources

For heathlands close to industrial areas there will be some input of phosphorus, albeit an unknown amount, from the deposition of aerosols and dust particles on foliage, plant litter and the soil surface. Some of these particles will enter the system to be cycled. Dust particles blown in from dirt roads or from nearby arable land can also increase the nutrient capital of heathland ecosystems. For example, Holstener-Jørgensen (1960), as quoted by Ovington (1962), found that the input

TABLE 16.1

Input of phosphorus in rainfall for a number of regions in Britain

Region	Rainfall ($cm\ yr^{-1}$)	Phosphorus ($kg\ ha^{-1}\ yr^{-1}$)	Reference
Scotland	95	0.19	Allen et al. (1969)
Northern England	*c.* 150	0.4	Allen (1964), Crisp (1966)
	116–150	0.77–0.97	Allen et al. (1969)
Western England	95	0.81	Allen et al. (1969)
Southern England	?	0.01	Chapman (1967)
Britain (five sites)	95–174	0.2 –1.0	Allen et al. (1968)

of all wind-borne material into a spruce woodland in Denmark amounted to about 1000 $kg\ ha^{-1}\ yr^{-1}$ at a distance of 80 m from the woodland edge. Most heathlands occur close to the coast and some phosphorus, though of unknown quantity, will enter the nutrient pool because of this maritime influence.

Movement of animals into the system from adjoining vegetation types may also increase the phosphorus capital, especially if there were isolated clumps of trees present to provide perches for birds or shelter or shade for mammals. Somerset (1975) observed the effect of excreta from an eagle's nest in changing the sclerophyll shrub vegetation under an isolated tree to an herbaceous pasture, and Specht (1975) commented, more generally, on the plant-ecological consequences of this increased level of fertility (in this case, mainly phosphorus level). For a *Calluna* heathland in Britain grazed by sheep, Robertson and Davies (1965) estimated a phosphorus input of about 0.06 $kg\ ha^{-1}\ yr^{-1}$ in the form of hay and mineral supplements.

Outputs

Erosion and deep drainage

The levels of phosphorus in deep drainage water from heathlands or in surface flow from wet *Calluna* heathlands are known from one example only for a moorland in northern England (Crisp, 1966). About 0.4 $kg\ ha^{-1}\ yr^{-1}$ phosphorus was lost in stream water, and the same amount was lost by movement of peat particles in solution out of the system. The amount of phosphorus lost by leaching and deep drainage may be greater on more permeable podzolized soils, and the amount lost by surface erosion (by wind and water) may be greater on steeply sloping land, such as occurs in southern California. Mooney and Parsons (1973) quoted data from Anderson et al. (1959) to show a total loss of particles from the surface soil of an area long unburned ranging from 440 to 1584 $kg\ ha^{-1}$ (yr^{-1}?), with significant levels occurring in the dry as well as the wet season. Some of this material is undoubtedly phosphorus, either adsorbed onto soil particles or as an organic complex formed from litter decomposition. Leeper (1957) estimated an annual loss of phosphorus in drainage water of 0.04% of the total phosphorus in the top 15 cm of, presumably, a podzolic soil. This estimate was made for an area in southeastern Victoria assuming an annual leaching rainfall of 640 mm.

Fire

A considerable literature exists on the loss of nutrients from burning of *Calluna* heathlands (Allen, 1964; Robertson and Davies, 1965; Allen et al., 1969). The estimates for loss of phosphorus show that it is small in amount relative to the loss of other nutrients, but considerable in amount relative to the input of phosphorus. For example, Robertson and Davies (1965) estimated a maximum loss of phosphorus from a *Calluna* heathland burnt on a 10-year rotation of only 7 $kg\ ha^{-1}$ (cf. 43 $kg\ ha^{-1}$ potassium) but this amount was of the order of 85 to 90% of the total phosphorus in the vegetation. Some of the phosphorus is lost as smoke (about 10 to 20% of the total lost, as estimated by Evans and Allen, 1971); most, however, is changed to ash, the phosphorus of which may be retained in the surface soil in an insoluble form, or it may be added by rapid leaching in an available form to the soil solution, or in very porous soils it may be leached out of the

root zone altogether. This ash formed as a result of burning may be lost to the system by wind or, more commonly, by surface movement after heavy rainfall.

Grazing and browsing

For *Calluna* heathlands, systematic removal of animal produce (sheep and gamebirds now, but cattle formerly) may represent some loss of phosphorus from the system. Robertson and Davies (1965) estimated a phosphorus loss of 0.1 kg ha^{-1} yr^{-1} owing to the sale of livestock and considered this to be extremely low compared with the potential losses from burning. On the other hand, Gimingham (1972) considered removal of animal produce "a significant loss . . . . but depletion due to burning is not particularly heavy". For moorland in northern England, Crisp (1966) assessed the relative importance of losses from downstream drift of invertebrates and from the sale of sheep. Phosphorus lost as the former was estimated at 0.005 kg ha^{-1} yr^{-1} and twice as much (0.01 kg ha^{-1} yr^{-1}) was lost as animal produce.

Other sources

At the wet end of the *Calluna* heathland spectrum, some phosphorus will be lost by harvesting and removal of peat. Allen (1964) estimated that removal in peat may amount to about 0.05 kg ha^{-1} yr^{-1} phosphorus. Peat harvesting is not generally, however, a characteristic feature of world heathlands.

Fluxes within heathlands

The level of inputs of phosphorus to heathland ecosystems is low over the short term (5 to 15 years) and there is a fair chance that, during such a time period, losses owing to fire and soil erosion may deplete these additions. Fluxes within the system thus become of considerable significance to a review of nutrient cycling in heathlands and this is true especially of phosphorus. Data on at least some of these fluxes in phosphorus cycling will now be reviewed.

Firstly, there is a flux between soil phosphorus available for plant growth and other forms of both inorganic and organic phosphorus in the soil, the chemistry and microbiology of which are too complex for this review. Heating of soil as occurs in a fire may often increase the availability of phosphorus, as Humphries (1966) showed. The phosphorus content (both total and "available") of the upper soil horizons is usually greater than that at depth, though in some soils the deep subsoil may be higher in phosphorus, depending on the composition of the parent rock and the clay content. For example, Specht et al. (1958) found a ten-fold increase in total phosphorus from the sandy A_3 horizon to the B horizon with a higher clay content. Leaching of soluble phosphate may occur through the profile, the extent of leaching over millennia depending mainly on the level of annual rainfall and soil type. Heathland soils are generally podzolized sands of varying depths from which phosphorus is readily leached.

By definition phosphorus available to plants is taken up by roots, or else it is incorporated in micro-organisms living in close association with the plant in the rhizosphere and then absorbed by the plant. Plant genera characteristic of heathlands often possess modifications to their root systems, such as ectotrophic mycorrhiza in myrtaceous plants (e.g. Chilvers, 1968), endotrophic mycorrhiza in genera of Epacridaceae and Ericaceae (e.g. McLennan, 1935; McNabb, 1961), and the so-called proteoid roots (Purnell, 1960) of most proteaceous genera, which increase the efficiency of soil phosphate uptake, or at least increase the root area in contact with the soil solution (Specht and Groves, 1966; Jeffrey, 1967). The root systems of heathlands explore fully the soil profile, as shown by Specht and Rayson (1957) for heathland in southeastern South Australia and Heath and Luckwill (1938) for upland *Calluna* heathland in Britain; thus, the chance for phosphate uptake is maximized. Incorporation of available soil phosphate into plant phosphate seems, therefore, to be an efficient process in heathlands.

Enhanced movement of phosphorus compounds from the root systems of those plants regenerating from root stocks occurred initially after a fire and continued until about ten years from fire (Specht et al., 1958). After this time the phosphorus content of root systems increased, sometimes at the expense of shoots, that is, translocation of phosphorus from root to shoot decreased in magnitude.

Within a shorter time period, Specht and Groves (1966) postulated an enhanced movement of phosphorus compounds, especially orthophosphate,

from senescing to developing tissue when shoot and leaf growth commenced. They provided some preliminary data in favour of this hypothesis from seedlings grown in water culture and from field-grown material but further documentation using field material is necessary. Although it was not tied in with seasonal growth, Harwood (1972) recorded a decrease by a factor of about eight in the phosphorus concentration between living and recently dead leaves of field-growing *Gymnoschoenus sphaerocephalus* (Cyperaceae), a characteristic plant of wet-heathlands in south-eastern Australia. If shoot extension of heathland species is mainly under the control of air temperature (given adequate moisture), then rising temperatures provide the trigger for this enhanced mobilization and translocation of phosphorus compounds out of senescing tissue prior to leaf fall. This flux of phosphorus is balanced, however, by the finding of Specht et al. (1958) that a large proportion (about 30%) of above-ground nutrients were found in *Banksia* (Proteaceae) fruits and *Xanthorrhoea* (Xanthorrhoeaceae) dead leaves. Some of this nutrient is phosphorus, which is thus effectively removed from the system until the next firing and represents a short-term immobilization at the expense of the phosphorus in actively growing tissue. The dynamic balance between phosphorus available for growth and development of vegetative and reproductive tissue in heathland plants is a topic for further research.

A significant flux in nutrient cycling of most plant communities, especially deciduous ones, is litter decomposition. How important is this to evergreen heathlands? Specht (1953) found the rate of accretion of phosphorus to the litter of a South Australian heathland to be 0.6 kg ha^{-1} yr^{-1} averaged over a 25-year period. Decomposition of litter in this environment took from 1.5 to 2.5 years, with decomposition in the first year after fire being very slow. In any one year the rate of decomposition was greatest over the late winter period, which is the time of maximal rainfall in a Mediterranean-type climate. Thus the phosphorus made available as a result of decomposition may be leached from the region of the surface roots. From the results of Specht (1953) we may conclude that there is a small recycling of phosphorus via the litter in heathlands and this will probably be of significance only when the litter is fired.

For this discussion we may neglect the flux in some nutrients which occurs between the foliage and the substrate when rainfall is intercepted and nutrients are leached out of the foliar canopy to be deposited in the litter and mineral soil. It has never been quantified for heathlands (unlike woodlands and forests), presumably because the foliar canopy is usually superimposed directly on the soil.

The phosphorus balance

Some of the inputs and outputs of phosphorus for heathland ecosystems are low in magnitude and of little significance in the short term. Others have the potential at least of being considerable, such as the loss of phosphorus as ash after burning, especially if the fire is followed by heavy rains. What is the overall balance obtaining over, say, a 10- to 15-year period? Several balance sheets have been compiled and they are summarized in Table 16.2 and discussed subsequently.

Of the relatively minor factors, it is assumed that rates of rock weathering and leaching are very slow and, therefore, the amount of phosphorus entering

TABLE 16.2

Phosphorus balance sheets for two heathlands dominated by *Calluna* (units are kg ha^{-1} except where stated otherwise)

Variable	Southern Britain	Northern Britain
Age of heathland (yr)	12	>10
Vegetation: leaf		2
stem	4	3
Litter	4	2
Total above-ground	8	7
Soil	37 (0–20 cm)	334 (0–15 cm)
% above-ground biomass and litter lost when fired	26%	
Remaining	6	
Lost	2	
Rainfall (yr)	0.01	
Rainfall (12 yr)	0.12	
Balance (gains–losses)	−2.1	−7*
Reference	Chapman (1967)	Robertson and Davies (1965)

* This value represents the maximum possible loss of phosphorus for *Calluna* heathland at three sites in northern England and strictly cannot be equated with the phosphorus capital in the heathland at Blanchland Moor given above. The actual extent of the loss will depend on fire intensity, as Robertson and Davies (1965) suggest.

the heathland ecosystem each year from this source is very low indeed and in terms of the growth of vegetation is of little significance. If one assumes a level of about 0.003% phosphorus in parent rock, as Beadle (1962) found for Hawkesbury Sandstone, and uses a mean content of about 0.002% phosphorus in the soil, very little phosphorus seems to have been lost by leaching or by re-sorting of particles in soils of eastern Australia. If it has, then it has been balanced by input from more recent weathering of parent rock and soil particles or by incorporation of decaying plant material.

Any discussion and quantification of soil phosphorus is beset, however, by a variety of qualifications, both biological and analytical. Within any one horizon, fluxes in soil phosphorus occur between inorganic and organically complexed phosphorus. The level of phosphorus available to the plant is difficult to quantify. The role of micro-organisms, especially those in the rhizosphere, in making soil phosphorus available to plant roots is poorly understood and may be very complex. For example, Mullette et al. (1974) hypothesized an interaction between root exudates, micro-organisms, aluminium ions and uptake mechanisms to account for a marked growth response to insoluble phosphates shown by a eucalypt growing on infertile heathland-type soil. The recirculation of available phosphorus through plants from subsoil to topsoil, whether because of root sloughing or deposition of soil-surface litter, is also poorly understood in quantitative terms. Whatever the level of soil phosphorus, it seems to be used efficiently by plants to maintain their growth and ensure their survival.

Other sources of input of phosphorus, such as grazing animal movements, may be important to the nutrient budget only locally and are rarely of general significance.

A significant input of phosphorus is that added annually as rainfall, which, though low, may be retained almost entirely by the vegetation and soil. More results are needed for shrublands in parts of the world other than Britain.

Phosphorus lost to the system by the outward movement of large wild herbivores (kangaroos and wallabies in Australia and deer or antelopes of different species in California, South Africa and northwestern Europe) can be assumed to equal the movement inward, until some data are gathered. Gimingham (1972) claimed that removal of carcases and wool of sheep was the largest loss proportionally, and for this reason nutrient losses from other grazing animals, such as gamebirds, have been ignored in constructing nutrient budgets for northern *Calluna* heathlands. The validity of this claim should be tested for these heathlands at least. Phosphorus lost as the products of grazing or browsing animals (both vertebrate and invertebrate) is probably only of minor significance in heathlands of other regions.

A major source of loss of phosphorus, although not adequately quantified, seems to be the loss of ash and surface soil particles when rains of high intensity sometimes follow summer burning of shrublands in Australia, South Africa and California, especially if they occur on steeply sloping land. By comparison, the magnitude of the loss by erosion of soil and ash is probably much less for European heathlands. And yet it is these latter heathlands for which nutrient budgets have been calculated in an effort to ascertain how much phosphorus may be lost following deliberate firing. Some details of two of these budgets are shown in Table 16.2.

On the basis of the phosphorus budgets presented in Table 16.2 and elsewhere (see Gimingham, 1972), it can be concluded that burning of *Calluna* heathlands every twelve years results in a small but significant loss of phosphorus from the ecosystem. This conclusion probably applies to other shrublands in other regions burnt at less regular intervals, although the magnitude of the loss may be greater if movement in solution of soil and ash particles occurs following fire and rainfall, for example as can happen in southern California. Firing of heathlands at shorter intervals may deplete the phosphorus status still further than that found for the documented examples of *Calluna* heathlands.

CALCIUM

Inputs

Rainfall

Robertson and Davies (1965) reported a range in the calcium content of rain water for three sites in Scotland of between 4 and 12 kg ha^{-1} yr^{-1}, with a mean of 7 kg ha^{-1} yr^{-1}. This level is in accord with

an estimated input of 9 kg ha $^{-1}$ yr $^{-1}$ for a wetter area in northern Britain. Other measured levels of calcium in rainwater in Britain range from 5 to 14 kg ha $^{-1}$ yr $^{-1}$, as given in table 28 of Gimingham (1972). Hutton and Leslie (1958) provided results of the same order of magnitude for Victoria for a series of stations at different distances from the coast. In all cases reported from Britain, the level of input was more than adequate to balance losses over a 10-year period when *Calluna* heathland was burnt.

Parent rock and soil

Most heathland soils and the parent rock from which they are derived are low in calcium. For example, Robertson and Davies (1965) measured a range from approximately 65 to 110 kg ha $^{-1}$ for the calcium content of a freely drained podzol under *Calluna* in Britain, and a higher level (590 kg ha $^{-1}$) for soil at a different site in the same region. A calcium level of 229 kg ha $^{-1}$ was reported by Chapman (1967) for the top 22 cm of a heathland soil in southern England. Soil calcium levels are usually low in acid soils, and heathland soils are characteristically acid.

Other sources

Some calcium may enter grazed *Calluna* heathlands as hay and mineral supplements for livestock, which Robertson and Davies (1965) estimated to be of the order of 0.2 kg ha $^{-1}$ yr $^{-1}$. The soil calcium status may be enhanced locally by the decomposition of animal bones, but this would rarely be of significance to the entire system. The deposition of aerosols and dust particles is another source of calcium, but of unknown significance for heathlands. It was found to be negligible for hardwood forests (Likens et al., 1967). Hutton (1956), as quoted by Hutton and Leslie (1958), postulated that dust from the dry surface of soils was a major source of calcium in inland areas of southern Australia. Heathlands are, however, generally coastal in this region, with the exception of southeastern South Australia.

Outputs

Erosion and deep drainage

As mentioned in connection with phosphorus, estimates for erosion from heathlands show it to be considerable but, with one exception, it has not been quantified for calcium. For soils at the wetter end of the range for heathlands in which peat may be present, some calcium will be lost as peat particles. Crisp (1966) measured as much as 4.8 kg calcium ha $^{-1}$ yr $^{-1}$ eroded from peaty soils and by far the major loss of calcium from this catchment was as Ca^{2+} in stream water. Apart from this one result I can find no other for loss of calcium in stream water from heathland catchments. Though there seems to be some loss of calcium by erosion and deep drainage from heathlands generally, for wet *Calluna* heathlands at least this net loss may be of only minor significance.

Fire

Burning of *Calluna* heathlands may lead to small losses of calcium, although the magnitude of the loss depends partly on the temperature of the burn. For example, Allen (1964) showed that although only 0.1% of the calcium originally in the vegetation was lost as a result of fire of "normal" temperatures (550° to 650°C), if fire temperatures were in the range 800° to 825°C up to 2.4% of the total calcium could be lost. Some of the calcium lost in a fire will be deposited as ash on the soil surface and some will be lost as smoke. The former fraction may re-enter the system, or be lost in leaching and/or run-off. The reader is referred to Allen (1964) and Allen et al. (1969), who endeavoured to quantify these losses by simulating experimentally a fire in *Calluna* heathland. Calcium as ash may not be lost as a result of burning as readily as some other elements, such as phosphorus. Chapman (1967) found, however, that 26% calcium in vegetation and litter was lost as smoke on burning — the same proportion as was lost as smoke for phosphorus.

Grazing and browsing

Crisp (1966) estimated 0.02 kg calcium ha $^{-1}$ yr $^{-1}$ to be lost from moorland owing to the sale of sheep and wool. Robertson and Davies (1965) estimated a loss of 0.1 kg calcium ha $^{-1}$ yr $^{-1}$ for the same factor, which is higher than Crisp's figure but still relatively small in relation to the level of inputs for *Calluna* heathlands.

Fluxes within heathlands

Fluxes of calcium within heathlands are similar

to those discussed already for phosphorus. This review is concerned with the differing rates of these fluxes; yet results on movement of calcium within heathland systems are almost unavailable, compared with results for phosphorus. This situation arises, presumably, because calcium is not known to be deficient for growth of heathlands in the field and therefore calcium cycling has received less attention.

Generally, where heathland occurs on deep acid sands the soil calcium available for plant growth decreases with depth. This is due presumably to accumulation by plants in the upper soil layers. If the B horizon is clayey the calcium level may be higher relative to the sandy upper horizon, as Specht et al. (1958) reported for southeastern Australia. Heating the surface soil as a result of fire may decrease the level of available calcium, depending on the temperature reached by the soil. Humphries (1966) showed very little change in calcium level if soil temperatures were below 300°C; but between 300° and 400°C there was a very marked decrease in calcium.

Of the soil calcium taken up by plants, Chapman (1967) found that the calcium concentration in a lowland *Calluna* heathland in southern Britain decreased up to about 20 years after fire and then was constant. In the same study the absolute amounts of calcium in the standing above-ground biomass increased linearly after about 10 years from fire. Because of the increased rate of litter decomposition after 10 years, the net accumulation of calcium in the standing above-ground biomass and litter decreased after about 15 years from fire. Similar trends are shown by the data of Robertson and Davies (1965) for almost pure *Calluna* heathland at Blanchland Moor, northern England.

Most of the data available on calcium fluxes are, however, for vegetation types other than heathlands and a brief discussion of these will now be attempted. The significance of some of the conclusions should be assessed for heathlands.

The relative mobility of nutrients in an evergreen sclerophyllous forest dominated by *Eucalyptus obliqua* (Myrtaceae) was studied by Attiwill (1964, 1968). The order of mobility was $Na > K > Ca > Mg > P$ and this was contrasted with the order found in Russian deciduous forests — namely, $K > P > Mg > Ca$. In the sclerophyll forest relatively more calcium was found in the heartwood and the litter, compared with phosphorus, indicating a lesser mobility of calcium in the tissues. Attiwill's data are confined to the dominant forest species. It is known, however, that some understorey species may be able to accumulate elements such as calcium, as Thomas (1969) showed for *Cornus florida* (Cornaceae) occurring in the understorey of a *Pinus taeda* forest. *Cornus* seedlings returned a greater percentage of total tree calcium to the forest floor in leaves than did the larger pine trees. As well, the rate of release of calcium from litter was rapid. Thomas (1969) pictured the role of *Cornus* seedlings in this system as being like "pumps" which keep calcium in circulation through the biologically active upper layers of soil. Such a mechanism may occur in heathlands, with their great diversity of species, but if so, it has yet to be described.

The calcium balance

From a review of the information available about calcium cycling in *Calluna* heathlands, Gimingham (1972) concluded that losses of calcium as a result of managing heathlands were more than adequately balanced by inputs. This appears a reasonable conclusion, and stands for the purposes of this present review. In any case, as the above shows, very little information is available for heathlands other than those dominated by *Calluna*. Calcium in rainfall is a major input and values from other heathlands with rainfall levels and intensities different from those of Britain should be collected. A further major input of calcium may be from weathering of parent rock. Shugart et al. (1976) estimated recently a seemingly high weathering rate of 16.9 kg $ha^{-1} yr^{-1}$ for a forested area in the eastern United States.

Some net losses of calcium from forested catchments have been reported (see, for example, Likens et al., 1967), but Chapman (1967) calculated a net gain in calcium of 43.5 kg ha^{-1} over a 12-year cycle in lowland *Calluna* heathland. His nutrient balance is reproduced in Table 16.3. The only other data available, although of a limited nature, are those of Lossaint (1973) for *garigue*, who found that calcium represented about two thirds of the annual input of all elements into a 17-year old shrubland. More results are needed obviously.

TABLE 16.3

Calcium balance sheet for a 12-year-old heathland in southern Britain dominated by *Calluna* (from Chapman, 1967)

Variable	Amount (kg ha^{-1})
Vegetation	33.0
Litter	15.2
Total above ground	48.2
Soil (0–20 cm)	229
% above-ground biomass and litter lost when fired	26%
Remaining	35.7
Lost	12.5
Rainfall (yr)	4.7
Rainfall (12 yr)	56
Balance (gains–losses)	+43.5

OTHER NUTRIENTS

Nutrients other than phosphorus and calcium play important roles in the growth of heathlands. In this section it is not intended to explore these roles in detail for each nutrient even if that were possible, but rather to highlight information on some of the other nutrients, especially nitrogen, sulphur and iron, as they affect growth and distribution of heaths.

Nitrogen

Cycling of nitrogen is significant because it involves a gaseous phase as well as a liquid (solute) phase. The nitrogen cycle is affected considerably by man's activities and, perhaps because of this, has been the subject of a level of research equivalent to that for phosphorus. Despite this, the conclusions that can be drawn from the results are even less clear than for phosphorus, as Gimingham (1972) has pointed out for *Calluna* heathlands.

In a series of papers, Hannon (1956, 1958, 1961) described nitrogen cycling in a mosaic of sclerophyll communities occurring on low fertility soils of the Sydney region, eastern Australia. Only a very small proportion of the total nitrogen capital was circulated annually (Hannon, 1958). Levels of total nitrogen in parent rock, surface soil and plant material were presented, together with available soil nitrogen, but these will not be considered in detail because most of the analyses apply to low eucalypt forest rather than heathland. Nitrogen levels in soil and plants for a heathland in southeastern South Australia at different ages from fire were presented by Specht et al. (1958). Specht et al. showed a negligible increment in total shoot nitrogen after about 17 years from fire, thereby emphasizing the recirculation of nitrogen within the mature system.

A nitrogen budget is available for a *Calluna* heathland. Chapman (1967) estimated a very substantial net loss of nitrogen from lowland heathland in southern Britain (viz. 111 kg ha^{-1}) over a 12-year fire rotation, largely he claimed, because of a loss as smoke of 95% of the nitrogen in above-ground biomass and litter on burning. This large loss was not balanced by the input of nitrogen in rainfall. Robertson and Davies (1965) estimated a similar rate of loss (119 kg ha^{-1}) to the system by burning on a 10-year rotation but some of this loss would be made good by input from rainfall. They estimated 60 kg ha^{-1} nitrogen for this period from rainfall giving a net loss of 59 kg ha^{-1} over 10 years. Robertson and Davies considered, however, that losses could be greater if the fire were hotter and thereby burn the litter layer as well. Allen (1964) found that well over half of the nitrogen in *Calluna* could be lost as smoke, and Evans and Allen (1971) reported an upper level of 57% nitrogen lost as smoke. Such results point to the need for measurement of fire intensity when considering losses of nitrogen as smoke.

An even greater deficiency in our understanding of nitrogen cycling in heathlands is the lack of results on the amount of nitrogen fixed by the species bearing root nodules which are a component of the flora especially strongly represented in Australian heathlands. In them, the dominant genera *Casuarina* and *Acacia* have been shown to fix nitrogen (Bowen, 1956; Bond, 1957, 1967). Halliday and Pate (1976) showed that the presence of the cycad *Macrozamia riedlei* contributed about 19 kg nitrogen ha^{-1} yr^{-1} to the *Eucalyptus–Banksia* sclerophyll woodland in which it occurred as an understorey species — a situation similar to heathland. In some *Calluna* heathlands *Ulex* spp. are often strongly represented (see, for example, Clark, 1968) and yet I can find no information on the rates of nitrogen fixation in nodules of these species. Egunjobi (1971) presented some information on nitrogen cycling in a *Ulex europaeus*

shrubland in New Zealand, but failed to quantify the amount of nitrogen fixed by symbiotic bacteria. In commenting on the nitrogen content of Australian heathland at different times from fire, Specht et al. (1958) made the interesting observation that the nitrogen-fixing species occurred early in the succession and then died out. In South African *fynbos*, however, very few nitrogen-fixing species are present even in the early stages of succession (R.L. Specht, pers. comm., 1976).

This discussion has so far highlighted only two important aspects of nitrogen cycling in heathlands. The subject of nitrogen availability in soil and its seasonal variation is another important aspect, which will not be discussed here. Nor will the important processes of volatilization and leaching of nitrogen, and the role of free-living nitrogen fixers, about which little is known for heathlands. Grazing of new shoots, often rich in nitrogen, may deplete the nitrogen of the system, especially if it follows soon after a fire. Gimingham (1972) rightly concluded that nitrogen cycling "...is a field which will certainly repay more intensive investigation".

Sulphur

Sulphur is included in this review because it is lost in appreciable amounts in smoke. As fire is one of the most common environmental factors affecting heathland composition and productivity (see Gill and Groves in Chapter 7 of this volume), the role of sulphur becomes significant. A further reason for including a brief discussion of sulphur is that in some heathland areas soil sulphur levels can limit growth of herbaceous communities, such as pastures. In eastern Australia, for example, Williams and Steinbergs (1958) presented results on sulphur (and phosphorus) levels in a range of soils and showed them to be deficient in sulphur, although acid soils and those of granitic origin common in heathlands were only slightly lower than the average for all soils. The similarity in the relative proportions of non-sulphate sulphur, carbon and nitrogen suggested a close relationship between sulphur and soil organic matter.

Losses of sulphur in smoke may be about 50% (Allen, 1964) at a moderate fire temperature (550° to 650°C), and up to 56% of the original sulphur content of *Calluna* was lost if fire temperatures reached 800°C. Such a large proportion lost as smoke may be made good by inputs in rainfall (up to 12 kg ha^{-1} yr^{-1} as reported by Allen, 1964), especially if the heathland is close to the coast or to a source of industry, as are many *Calluna* heathlands. In regions where the inputs may be less, for instance southeastern South Australia, and where fire frequency (and intensities?) may be greater, a sulphur budget is essential information for heathland management. The lack of results on sulphur is a serious omission from the otherwise fairly complete study of nutrient cycling in the Dark Island heathland described by Specht et al. (1958).

Iron

So far this review has not considered the interaction between water status and nutrient availability. This interaction is important for the growth and distribution of heathland species at the wetter end of the soil-moisture spectrum, and particularly those species occurring in seasonally waterlogged sites. Waterlogging affects the availability of many nutrients but it has been shown to affect especially iron uptake by heathland plants. Jones and Etherington (1970) grew two *Erica* species under waterlogged and drier conditions and showed that both species took up significantly more iron from the wetter soil. *E. cinerea* occurs naturally in drier sites, was killed rapidly by waterlogging and was shown to take up more iron than *E. tetralix* occurring naturally in so-called wet-heathlands. In an experiment with cut shoots both Fe^{2+} and Fe^{3+} produced similar results which led the authors to suggest that high iron levels rather than Fe^{2+} *per se* may be causing the symptoms associated with waterlogging and death of *E. cinerea*. Studies of iron nutrition of species pairs in other genera, from other regions — for instance *Banksia serratifolia* and *B. robur* in eastern Australia — may help further to reveal a significant role for iron in the relative distribution of heathland species in sites of seasonally different water status.

CONCLUSIONS

Any discussion of nutrient cycling must be less than satisfactory if nutrients are considered indi-

vidually, as they have been in this review. It is the interactions between different nutrients, and their interactions in turn with other factors, such as fire and soil moisture, which often determine composition and productivity of different plant communities. For example, although iron was singled out for discussion in relation to the distribution of wet-heathland species, Jones and Etherington (1970) also considered manganese. Loach (1966), in a similar study of the relative distribution of some wet-heathland species, considered nitrogen, potassium and phosphorus nutrition in relation to high soil moisture levels, but did not consider iron or manganese. At the end of a series of three papers on nitrogen cycling in sclerophyll communities in eastern Australia, Hannon (1961) concluded "that the nitrogen economy of these communities is controlled by an efficient phosphorus régime", and thus transferred the emphasis from nitrogen alone to the interaction between nitrogen and phosphorus. In discussing and measuring nutrient levels in plant systems let us not overlook the interactions between nutrients.

The framework in which nutrient cycling has been discussed in this review is that of the soil–plant system with its various inputs and outputs. While these have been quantified to extents varying with each of the nutrients considered, it has been a constant theme that data for heathlands are few relative to those for some other soil–plant systems. It is of concern that several recent and expensive ecosystem ("biome") studies launched under the aegis of the International Biological Program, especially in the United States, have failed to consider heathlands.

Of the many unknowns associated with nutrient cycling in heathlands some major ones which should be accorded high priority for future research include: (1) measurement of the nutrient content of rainfall, especially for heathlands near the coast; (2) a study of the rates of nitrogen fixation by heathland species in relation to nitrogen cycling in heathlands; (3) studies of litter decomposition and its role in nutrient cycling compared with the redistribution of nutrients within shrubs; (4) the quantification of nutrient losses when heathlands are burnt (this is especially needed for heathlands other than *Calluna* heathlands, about which some information is available already); and (5) an assessment of the role of invertebrate "grazing". Crisp (1966) quantified this process for a moorland. Phytophagous insects have a significant effect on productivity of some sclerophyll communities, for example eucalypt plantations in eastern Australia (Carne et al., 1974), and may increase the rate of flux of nutrients. A similarly significant role may be postulated for invertebrates in heathlands.

Despite the relative paucity of results, what may be concluded on a more positive note concerning nutrient cycling in heathlands and related shrublands? One conclusion is that nutrients in rainfall alone may, in some cases, be sufficient to balance any losses from the system. This conclusion applies to the relatively immobile elements in heathlands, of which calcium has been chosen as an example for this review. Another conclusion is that some of the relatively mobile ions, such as phosphate, may be cycled within heathlands very efficiently. Two steps in the phosphorus cycle seem especially efficient: firstly, the uptake of soil-solution phosphorus as it is modified anatomically and physiologically by micro-organisms and specialized root structures; and secondly, the seasonal translocation of phosphate from senescing to developing shoot tissues. Specht and Groves (1966) discussed these two aspects for some Australian heathland species, but more detailed studies have still to be initiated.

Fire and surface soil erosion appear to be the most important sources of nutrient loss; this is especially so if the two factors interact when intense summer rain storms follow fire, as they may do in eastern Australia. This conclusion applies to nutrients lost as ash particles. Nutrients such as nitrogen and sulphur will also be lost as smoke to varying extents depending on fire temperature. Grazing or browsing seem to be a significant source of nutrient loss only if it follows soon after a fire.

ACKNOWLEDGEMENTS

Drs. A.R. Aston, A.M. Gill, C.H. Williams, all of C.S.I.R.O. Division of Plant Industry, Canberra, and Mr. C.E. Harwood, Australian National University, Canberra, helped with comments on an earlier draft of this review.

REFERENCES

Allen, S.E., 1964. Chemical aspects of heather burning. *J. Appl. Ecol.*, 1: 347–367.

Allen, S.E., Carlisle, A., White, E.J. and Evans, C.C., 1968. The plant nutrient content of rainwater. *J. Ecol.*, 56: 497–504.

Allen, S.E., Evans, C.C. and Grimshaw, H.M., 1969. The distribution of mineral nutrients in soil after heather burning. *Oikos*, 20: 16–25.

Anderson, H.W., Coleman, G.B. and Zinke, P.J., 1959. Summer slides and winter scour–dry–wet erosion in southern California mountains. *U.S. For. Serv., Pacific Southwest For. Ra. Exp. Station, Tech. Pap., No. 36*: 12 pp.

Attiwill, P.M., 1964. *Studies of Soil Fertility and Plant Nutrition in* Eucalyptus obliqua *L'Hérit.* Thesis, University of Melbourne, Vic., 334 pp.

Attiwill, P.M., 1966. The chemical composition of rainwater in relation to cycling of nutrients in mature *Eucalyptus* forest. *Plant Soil*, 24: 390–406.

Attiwill, P.M., 1968. The loss of elements from decomposing litter. *Ecology*, 49: 142–145.

Beadle, N.C.W., 1962. An alternative hypothesis to account for the generally low phosphate content of Australian soils. *Aust. J. Agric. Res.*, 13: 434–442.

Bond, G., 1957. The development and significance of the root nodules of *Casuarina*. *Ann. Bot.*, 21: 373–380.

Bond, G., 1967. Fixation of nitrogen by higher plants other than legumes. *Annu. Rev. Plant Physiol.*, 18: 107–126.

Bormann, F.H. and Likens, G.E., 1967. Nutrient cycling. *Science*, 155: 424–429.

Bowen, G.D., 1956. Nodulation of legumes indigenous to Queensland. *Qld. J. Agric. Anim. Sci.*, 13: 47–60.

Carne, P.B., Greaves, R.T.G. and McInnes, R.S., 1974. Insect damage to plantation-grown eucalypts in north coastal New South Wales, with particular reference to Christmas beetles (Coleoptera: Scarabaeidae). *J. Aust. Entomol. Soc.*, 13: 189–206.

Chapman, S.B., 1967. Nutrient budgets for a dry heath ecosystem in the south of England. *J. Ecol.*, 55: 677–689.

Chilvers, G.A., 1968. Some distinctive types of eucalypt mycorrhiza. *Aust. J. Bot.*, 16: 49–70.

Clark, S.C., 1968. The structure of some *Ulex gallii* heaths in eastern Ireland. *Proc. R. Ir. Acad.*, 66B: 43–51.

Crisp, D.T., 1966. Input and output of minerals for an area of Pennine moorland: the importance of precipitation, drainage, peat erosion and animals. *J. Appl. Ecol.*, 3: 327–348.

Delwiche, C.C., Zinke, P.J. and Johnson, C.M., 1965. Nitrogen fixation by *Ceanothus*. *Plant Physiol.*, 40: 1045–1047.

Egunjobi, J.K., 1971. Ecosystem processes in a stand of *Ulex europaeus* L. II. The cycling of chemical elements in the ecosystem. *J. Ecol.*, 59: 669–678.

Evans, C.C. and Allen, S.E., 1971. Nutrient losses in smoke produced during heather burning. *Oikos*, 22: 149–154.

Gimingham, C.H., 1972. *Ecology of Heathlands*. Chapman and Hall, London, 266 pp.

Halliday, J. and Pate, J.S., 1976. Symbiotic nitrogen fixation by coralloid roots of the cycad *Macrozamia riedlei*: physiological characteristics and ecological significance. *Aust. J. Plant Physiol.*, 3: 349–358.

Hannon, N.J., 1956. The status of nitrogen in the Hawkesbury Sandstone soils and their plant communities in the Sydney district. I. The significance and level of nitrogen. *Proc. Linn. Soc. N.S.W.*, 81: 118–143.

Hannon, N.J., 1958. The status of nitrogen in the Hawkesbury Sandstone soils and their plant communities in the Sydney district. II. The distribution and circulation of nitrogen. *Proc. Linn. Soc. N.S.W.*, 83: 65–85.

Hannon, N.J., 1961. The status of nitrogen in the Hawkesbury Sandstone soils and their plant communities in the Sydney district. III. The sources of loss of nitrogen. *Proc. Linn. Soc. N.S.W.*, 86: 207–216.

Harwood, C.E., 1972. *Aspects of Mineral Cycling in Tasmanian Ecosystems*. Thesis, University of Tasmania, Hobart, 145 pp.

Heath, G.H. and Luckwill, L.C., 1938. The rooting systems of heath plants. *J. Ecol.*, 26: 331–352.

Holstener-Jørgensen, H., 1960. Indfygning af jord i en plantages vestrand. *Forstl. Forsøksv. Danm.*,26: 391–397.

Humphries, F.R., 1966. Some effects of fire on plant nutrients. In: *The Effects of Fire on Forest Communities. N.S.W. For. Comm. Tech. Pap.*, No. 13: 53–59.

Hutton, J.T., 1956. The chemistry of rainwater with particular reference to conditions in South Eastern Australia. In: *Australia UNESCO Symposium on Arid Zone Climatology with Special Reference to Microclimatology, Canberra, October 1956. Papers from Australia and New Zealand*, pp. 34a–34i.

Hutton, J.T. and Leslie, T.I., 1958. Accession of non-nitrogenous ions dissolved in rainwater to soils in Victoria. *Aust. J. Agric. Res.*, 9: 492–507.

Jeffrey, D.W., 1967. Phosphate nutrition of Australian heath plants. I. The importance of proteoid roots in *Banksia* (Proteaceae). *Aust. J. Bot.*, 15: 403–411.

Jones, H.E. and Etherington, J.R., 1970. Comparative studies of plant growth and distribution in relation to water-logging. I. The survival of *Erica cinerea* L. and *E. tetralix* L. and its apparent relationship to iron and manganese uptake in waterlogged soil. *J. Ecol.*, 58: 487–496.

Leeper, G.W., 1957. *Introduction to Soil Science*, Melbourne University Press, Melbourne, Vic., 3rd ed., 222 pp.

Likens, G.E., Bormann, F.H., Johnson, N.M. and Pierce, R.S., 1967. The calcium, magnesium, potassium, and sodium budgets for a small forested ecosystem. *Ecology*, 48: 772–785.

Loach, K., 1966. Relations between soil nutrients and vegetation in wet heaths. I. Soil nutrient content and moisture conditions. *J. Ecol.*, 54: 597–608.

Lossaint, P., 1973. Soil-vegetation relationships in Mediterranean ecosystems of southern France. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems: Origin and Structure*. Chapman and Hall, London, pp. 199–210.

McLennan, E.I., 1935. Non-symbiotic development of seedlings of *Epacris impressa* Labill. *New Phytol.*, 34: 55–63.

McNabb, R.F.R., 1961.Mycorrhiza in the New Zealand Ericales. *Aust. J. Bot.*, 9: 57–61.

Mooney, H.A. and Parsons, D.J., 1973. Structure and function of the California chaparral — an example from San Dimas. In: F. di Castri and H.A. Mooney (Editors), *Mediterranean Type Ecosystems: Origin and Structure*. Chapman and Hall,

London, pp. 83–112.

Mullette, K.J., Hannon, N.J. and Elliott, A.G.L., 1974. Insoluble phosphorus usage by *Eucalyptus*. *Plant Soil*, 41: 199–205.

Ovington, J.D., 1962. Quantitative ecology and the woodland ecosystem concept. *Adv. Ecol. Res.*, 1: 103–192.

Purnell, H.M., 1960. Studies of the family Proteaceae. I. Anatomy and morphology of the roots of some Victorian species. *Aust. J. Bot.*, 8: 38–50.

Robertson, R.A. and Davies, G.E., 1965. Quantities of plant nutrients in heather ecosystems. *J. Appl. Ecol.*, 2: 211–220.

Shugart, H.H., Riechle, D.E., Edwards, N.T. and Kercher, J.R., 1976. A model of calcium-cycling in an East Tennessee *Liriodendron* forest: model structure, parameters and frequency response analysis. *Ecology*, 57: 99–109.

Somerset, H.B., 1975. Ecology of an eagle's nest. *Search*, 6: 154.

Specht, R.L., 1953. *The Ecology of the Heath Vegetation in the Upper South-East of South Australia*. Thesis, University of Adelaide, Adelaide, S.A., 143 pp.

Specht, R.L., 1969. A comparison of the sclerophyllous vegetation characteristic of mediterranean type climates in France, California, and southern Australia. II. Dry matter, energy, and nutrient accumulation. *Aust. J. Bot.*, 17: 293–308.

Specht, R.L., 1975. The effect of fertilizers on sclerophyll (heath) vegetation — the problems of revegetation after sand-mining of high dunes. *Search*, 6: 459–461.

Specht, R.L. and Groves, R.H., 1966. A comparison of the phosphorus nutrition of Australian heath plants and introduced economic plants. *Aust. J. Bot.*, 14: 201–221.

Specht, R.L. and Rayson, P., 1957. Dark Island Heath (Ninety-Mile Plain, South Australia). III. The root systems. *Aust. J. Bot.*, 5: 103–114.

Specht, R.L., Rayson, P. and Jackman, M.E., 1958. Dark Island Heath (Ninety-Mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight, and mineral nutrient status. *Aust. J. Bot.*, 6: 59–88.

Thomas, W.A., 1969. Accumulation and cycling of calcium by dogwood trees. *Ecol. Monogr.*, 39: 101–120.

Wild, A., 1961. A pedological study of phosphorus in 12 soils derived from granite. *Aust. J. Agric. Res.*, 12: 286–299.

Williams, C.H. and Steinbergs, A., 1958. Sulphur and phosphorus in some eastern Australian soils. *Aust. J. Agric. Res.*, 9: 483–491.